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BULLETIN
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On the Structure of the Testa of Several Leguminous Seeds.

By L. H. Pammel.

Plates LII and LIII.

The structure of the seed-coats of numerous *Leguminosæ* has been studied by several able observers,[*] but as their observations relate in the main to thin-walled seeds, like those of *Phaseolus*, *Pisum* and *Vicia*, I undertook an examination of the exceedingly hard seeds of the Kentucky Coffee Tree, and of the Sea Bean and Calabar Bean at the suggestion of Prof. Trelease, in whose laboratory the work was done. I am greatly indebted to him for many suggestions in connection with the work, as well as for the use of literature on the subject. The common garden bean, or haricot bean, *Phaseolus vulgaris*, has been taken as illustrating the typical structure of the leguminous seed. Haberlandt has fully described the structure and development of the seed-coats of *Phaseolus*,[*] but the following resumé of the results of my own examination, though agreeing in general with his statements, is given to facilitate comparison when the other seeds are described:

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[*] J. Gaertner, "De Fructibus et Seminibus Plantarum," 1791, ii., p. 325, describes the seeds of *Vicia pisiformis*, *V. nodosa*, *V. biennis*, *V. hybrida*.

G. W. Bischoff, Handbuch der bot. Terminologie und Systemkunde, 1883, Taf. XLIII., Fig. 1869.

M. J. Schleiden und J. R. Th. Vogel, Ueber das Albumen insbesondere der Leguminosen. Nov. acta d. Leop. Carol. Academ. xix., pt. II., p. 51.

F. Nobbe, Handbuch der Samenkunde, 1876, pp. 79–80 and 84, figures and describes the seed-coats of *Medicago sativa*, *Trifolium pratense* and *Vicia faba*.

A. Sempolowski, Beitraege zur Kenntniss des Baues der Samenschale. Inaugural dissertation, Leipzig, 1874, 3 Taf.

J. Chalon, La graine des Legumineuses, (1) cellules de la carapace, (2) albumen, Mons, 1875.

M. G. Monnier, Recherches sur la nervation de la graine. Ann. des Sciences Naturelles, 5 series, xvi., 1872, p. 233.

Günther Beck, Vergleichende Anatomie der Samen von *Vicia* und *Ervum*. Kaiserlichen Akademie der Wissenschaften, Wien, 1878, lxxvii., I. Abtheilung, p. 545, 2 Taf.

R. Junawiez, Die Lichtlinie in den Prismencellen der Samenschalen. Kaiserlichen Akademie der Wissenchaften, Wien, 1877, I Abth, lxxvi., p. 335, 2 Taf.

Georg Lohde, Ueber die Entwickelungsgeschichte und den Bau einiger Samenschalen. Inaugural dissertation, Leipzig, 1874, 2 Taf.

Joh. Friedrich Fickel, Ueber die Anatomie und Entwickelungsgeschichte der Samenschalen einiger *Cucurbitaceen*. Inaugural dissertation, Leipzig, 1876, 2 Taf.

THE COMMON GARDEN BEAN (*Phaseolus vulgaris*, Savi.)—In the seed-coats of the common garden bean there are five well-marked layers: I. The palisade layer. II. The crystal layer. III. A layer of simple parenchyma. IV. A layer in which the fibro-vascular elements are found, surrounded by parenchyma. V. A layer of very compact branched cells.

The cuticle covering the palisade cells, as described by Haberlandt, is very hard to distinguish because of its tenuity and the difficulty involved in getting sections which are thin enough, while in some varieties it has a tendency to flake off.

The prismatic palisade cells are five, six or more sided, and in a surface view show a branched cell cavity (Fig. 1). In a cross section of the seed-coats (Fig. 2) the cells are seen to be greatly elongated radially. The central cell cavity, which is somewhat widened at the base, extends nearly the entire length of the cell to the cuticle (Fig 3).† As a consequence of this gradual widening, the lateral walls gradually become thinner towards the base (Figs. 3 and 4).

In an isolated palisade cell, macerated in concentrated potash, or in Schultze's medium, the structure of the folds and the cell cavity are more clearly indicated, as shown in Figs. 3 and 4.

In the colored varieties of *Phaseolus*, the cell cavities are filled with a pigment. The narrow "light line" runs close under the cuticle (Fig. 2, 1^a.)‡

In a surface view the cells of the second layer are five or six sided, very thick-walled, and the cavity appears to be filled with a crystal of calcium oxalate.§

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*G. Haberlandt, Ueber die Entwickelungsgeschichte und den Bau der Samenschale bei der Gattung *Phaseolus*. Separat abdruck aus den Sitzungsbericht der Kais. Akad. der Wiss.; Wien, 1877, lxxvi., I. Abth.

†There are some apparent exceptions to this, as in some cases this portion of the cavity seemed only to extend up about one-third of the distance.

‡ *Sicyos angulatus* is said to have peculiar refractive portions so characteristic of *Leguminosæ*, but they are present in the third layer. (See Fickel, l. c., p. 11, Plate I., Fig. 22.)

§In some of the varieties of *Phaseolus vulgaris* the cells present a different appearance, since they do not contain crystals. The inner layer of parenchyma cells in the seed-coats of *Sicyos angulatus* contain, according to Fickel (l. c., p. 11) crystals of calcium oxalate in the course of their development, but these disappear when the seed has fully ripened.

In a radial section (Fig. 2, II) the crystals, which are often twinned, fill more or less completely the I-shaped cavity, which is almost obliterated by the swollen lateral walls where it is not distended by them.

The cells of the third layer are elongated laterally, are thin-walled and separated by numerous intercellular spaces. In a tangential section they are star-shaped. The cell cavities are filled with fine granular protoplasm. Some of these cells in the colored varieties contain pigment.

The cells of the fourth layer are elongated laterally and are also thin-walled; they differ from those of the third layer in that the cells are longer and larger. In colored varieties some of these cells contain pigment. The fibro-vascular elements are present in this layer.

The cells of the last layer are very compact and appear small in a radial section. However, their true structure can only be determined in a tangential section, when the cells are seen to resemble somewhat the star-shaped cells of the third layer, but they differ from those in that they are more dichotomously branched. The cell contents are made up of fine, granular protoplasm.

THE KENTUCKY COFFEE BEAN (*Gymnocladus Canadensis*, Lam.)—The seed of the Kentucky Coffee Tree is anatropous and has a straight embryo. With a small magnifying glass there can be readily distinguished three distinct layers in the seed-coats. The innermost of these is the thickest and darkest layer (Fig. 5). On the upper flattened side it generally diminishes in thickness as it approaches the poles of the seed. Above the palisade layer is the rather thickened cuticle, which has a tendency to separate from the palisade cells. This layer when macerated in water and allowed to stand, sometimes breaks up into small pieces and separates from the remaining part of the seed-coat. It is then somewhat mucilaginous. In a surface view the palisade cells are much the same as in *Phaseolus*, excepting that the central cavity (Fig. 6) is greatly enlarged and the folds are less distinct and marked as regards their branching. In a cross section (Fig. 7) six well-defined layers may be distinguished. I. The palisade layer. II. A layer of I-shaped cells. III. A layer of sclerenchyma. IV. A layer carrying pigment. V. A layer of vessels and thick-walled parenchyma. VI. A layer of star-shaped parenchyma-cells.

The palisade cells are greatly elongated radially; the lateral walls are thickened as in *Phaseolus*, but more uniformly, because of the uniformity of the cell cavity (Figs. 8, 9 and 10). In Figs. 7, 8, 9 and 10 at *b*, several prominent rounded points may be seen which refract light very strongly. This appearance is not affected when the cells are macerated in potash, or Schultze's medium, or when allowed to decay, somewhat, in water. The cell cavity is slightly enlarged at the base (Figs. 7, 8, 9 and 10, at *d*.), diminishing in calibre upward to *e*, when it again begins to enlarge to the point *b*. From *a* to the cuticle the cell cavity is faint and can only be definitely made out in stained sections.*

The folds are from two to eight in number and vary greatly in their length and manner of joining the cell cavity. In Figs. 8, 9 and 10 the refractive points are shown; they have the same peculiarity that the cell-cavity has. From *b* to the cuticle (Figs. 8, 9 and 10) the folds are very faint, and can only be distinctly seen after staining. In the lower portion of the palisade cells (Figs. 8 to 10) are several slight folds which generally arise gradually. After they have attained considerable breadth they begin to diminish in size and end as fine threads. Sometimes they are apparently disconnected from the cell cavity, as in Fig. 8, and in some cases they have more than one of these fine endings. There are two well-developed light lines on these cells,† a wide and a narrow one. The wide light line begins close under the cuticle, extends to the refractive points (Fig. 7, *a-b*), and is lighter in its upper than in its lower portion. The narrow line (Fig. 7, *c*) is situated slightly above the central part of the palisade cells and has a much clearer definition than the broad line. The second layer is made up of I-shaped support-cells, homologous with the crystal layer of *Phaseolus*, but having numerous intercellular spaces. The cavity of these cells is very narrow at the middle (Fig. 7, II., *e*), enlarging as it reaches the upper and lower cross-bar, thus giving to it also the shape of an I. The third layer differs remarkably from any of the others; the cells are more or less elongated laterally, that is, in the direction of the seed-coat. The cell walls are greatly thickened and are beautifully pitted. The cell cavity is very narrow, and often has an irregular outline with peculiar markings. The cells of this layer change somewhat in size and shape as they are followed inwardly, becoming more like the parenchyma of the fifth layer. The fourth is a very narrow layer and carries a brownish-yellow pigment. This is followed by the fifth layer, which is made up of a comparatively thick-walled parenchyma; well-developed spiral vessels are also found in it.

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*The fluids used were methyl violet and chloriodide of zinc.

†I shall speak of their behavior with micro-chemical tests in another connection.

The sixth layer may be divided into two parts. In the first the intercellular spaces are small, while in the second they are large and numerous. The first part (*f*) is made up of thick-walled, star-shaped cells, which have an irregular outline (Fig. 11). The cell walls are thickened irregularly, as shown in the figure. There are from one to four pits in a cell wall; sometimes these pits are small and narrow (Fig. 11., *b*). A number of oil globules are usually distributed through the protoplasm of each cell. The cells of the second portion (*g*) of the sixth layer are star-shaped in a tangential section, and have the same peculiar pitted walls as those of *f*. The cell walls of one kind of these cells are thinner than those of *f*, while the cells of a second kind have as thick walls as those of *a*, Fig. 11. The protoplasm is very granular and has oil globules distributed through it.

THE CALABAR BEAN (*Physostigma venenosum*, Balf.)—There is a marked difference between the seed-coats of *Gymnocladus* and those of the calabar bean. The former, when soaked in water, become mucilaginous and fragile, whereas the seed-coats of the latter are coriaceous and somewhat flexible and have some affinities with those of the sea bean.

In a surface view the palisade cells are five or six sided and very often elongated (Fig. 13). The folds are often branched equilaterally, as in Fig. 12, or are of an abnormal form, as shown in Fig. 13. A peculiar feature of these palisade cells, macerated in concentrated potash, is that they show numerous intersecting striations (Figs. 14 and 15) running obliquely, or almost horizontally, about the cells.* The cell cavity is quite uniform in breadth, gradually diminishing upwards, as in Fig. 14, or sometimes quite abruptly, as in Fig. 15. In some cells the cavity plainly extends to the cuticle, though in others it cannot be traced so far. A number of folds run down into the lateral walls, rarely, however, obviously entering the cell cavity as in *Phaseolus* or *Gymnocladus*.

The I-shaped support-cells (Fig. 16, II.) are similar to those of *Gymnocladus*, though the intercellular spaces and I-shaped cavities of the cells are frequently larger. The third evident layer (Fig. 16, III.) is made up of loose, thick-walled cells with numerous intercellular spaces. The cells of the fourth layer are rather more compact, are elongated laterally and carry the brown pigment.

THE SEA BEAN (*Mucuna urens.*)—The seed-coat of the sea bean is exceedingly hard, but is only composed of two well defined layers; a palisade layer, having a brownish color, and a layer of loose parenchyma, the cell walls of which are colored dark brown.

In a surface view (Fig. 17) the palisade cells are five or six sided, with the characteristic foldings of *Phaseolus* and *Gymnocladus*, excepting that the central portion is greatly enlarged. In most cases the folds terminate in the angles of the cells and are often slightly enlarged. In a cross section of the seed-coat (Fig. 18,) the thickened cuticle of the palisade layer is well defined (*a*,) as is also the light line (Fig. 18, *b*) which runs close under the cuticle and is somewhat broader than in the calabar bean. In an isolated palisade cell (Figs. 19, 20 and 21) the cavity is seen to extend to the cuticle; it is much wider at the base than is the cell cavity of the calabar bean. At Fig 20, *a*, it is indistinct and small; it, however, gradually enlarges upwards until it reaches the cuticle, where it attains considerable breadth. The outline of the cell cavity is irregular and wavy. The folds extending into the lateral walls are very variable; some are very short, as in Fig.

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*According to A. Sempolowski, l. c., p. 26, Plate II., Fig. 16, the palisade cells of the seed-coats of *Lupinus angustifolius*, *L. luteus.*, *L. albus*, *L. hirsutus*, *L. pilosus*, and *L. Cruikshankii* have, in the lower part of the cell, what he has called pore-canals, in the form of the cross-striations which I have described in the calabar bean. The cross-striations of the calabar bean are plainly not pore-canals.

20; others straight and longer, as in Fig. 19. Though small, the folds are well defined. The same clear definition was also obtained in a surface view of the palisade cells. In none of the specimens studied could the outlines of the cell walls, their cavities, or of the folds be made out as in this species. The palisade cells show a slight indication of the characteristic striations of those of the calabar bean.

The second layer (Fig. 18, II) may be divided into two parts. The first of these is a single layer of cells homologous with the crystal layer of *Phaseolus* and the I-shaped layer of *Gymnocladus* and *Physostigma.** But according to A. Sempolowski (l. c., pp. 28, 30), the second layer is not identical in its structure with the layers which follow, but has the true support-cells. There are certainly gradations from true support-cells to the parenchyma which follows in many of the *Leguminosæ.* (G. Beck and others.)

The cells of this layer differ from those that follow in that they are much thicker walled and have a small cell cavity. They are separated by narrow and large intercellular spaces. The fibro-vascular elements are present in the lower portion of this layer.

These are the chief characteristics of the seed-coats under consideration. From the account which has been given, it will be seen that the hard-walled leguminous seeds do not differ much in the nature and arrangement of their protecting envelopes from those of a less resistant character, their greater firmness depending usually upon the greater development of one or more of the layers which are normally present, and upon differences in the nature of the walls of their component cells. The microchemical behavior of the walls in the several cases, and especially certain interesting peculiarities of the refractive portions constituting the so-called light lines, must, however, be reserved for consideration in another place.

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*According to Nobbe, Samenkunde, p. 79, the cells between the palisade layer and aleurone layer of *Trifolium pratense*, and *Medicago sativa* are identical in structure, excepting the fibro-vascular elements carried in the lower portion of the layer.

Günther Beck (l. c., p. 547), speaks of the "Hartschichte" and the "Quellschichte"; in the latter he places (1) the I-shaped support-cells, (2) the true absorbing tissue, (3) the fibro-vascular elements and their surrounding tissue.

EXPLANATION OF PLATES.

Figs. 1-4. *Phaseolus vulgaris.*

Fig. 1. Surface view of palisade cell; × 700.

Fig. 2. Cross section of seed-coat; × 120. I. Palisade layer; *a*, narrow light line. II. Crystal layer. III. Layer of simple parenchyma. IV. Layer of parenchyma, containing fibro-vascular elements. V. Layer of compact, branched cells. VI. Aleurone layer. VII. Starch layer.

Figs. 3-4. Isolated palisade cells, macerated in potash; × 250.

Figs. 5-11. *Gymnocladus Canadensis.*

Fig. 5. Cross section of bean; natural size.

Fig. 6. Surface view of palisade cell; × 700.

Fig. 7. Cross section of the seed-coat; × 120. I. Palisade layer; *a*, cuticle; *b*, wide light line; *c*, refractive points; *d*, narrow light line. II. I-shaped support-cells. III. Sclerenchyma cells. IV. Pigment layer. V. Layer of thick-walled parenchyma and spiral vessels. VI. Layer of star-shaped parenchyma cells; *f*, upper portion; *g*, lower portion. VII. Aleurone layer.

Figs. 8, 9 and 10. Isolated palisade cells, macerated in potash; × 175; *b*, refractive points.

Fig. 11. Cells of upper portion of VI. layer; × 350.

Figs. 12-16. *Physostigma venenosum.*

Figs. 12 and 13. Surface view of palisade cells; × 700.

Figs. 14 and 15. Isolated palisade cells, macerated in potash; × 175.

Fig. 16. Cross section of seed-coat; × 120. I. Palisade layer; *a*, cuticle; *b*, light line. II. I-shaped cells. III. Loose, thick-walled parenchyma. IV. Pigment layer.

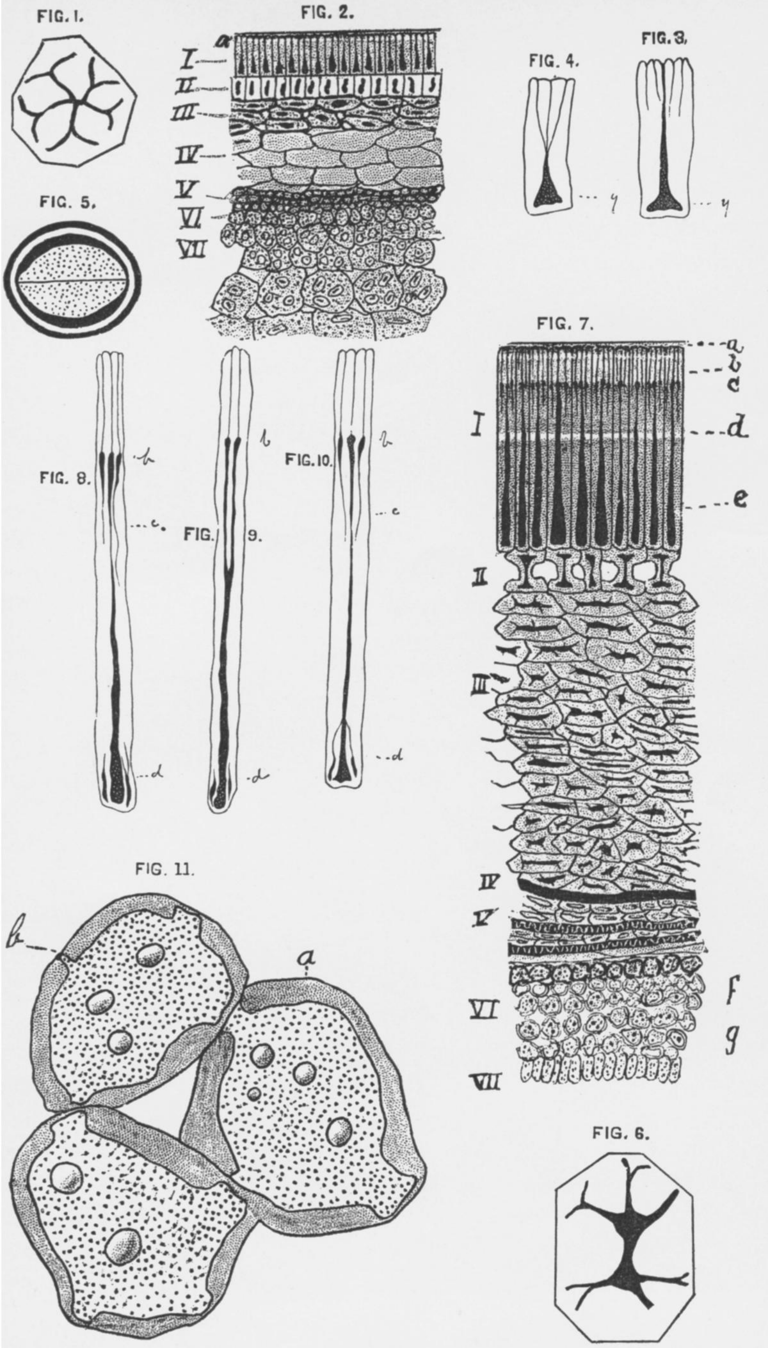
Figs. 17-21. *Mucuna urens.*

Fig. 17. Surface view of palisade cell; × 700.

Fig. 18. Cross section of seed-coat; × 120. I. Palisade layer; *a*, cuticle; *b*, light line. II. *c* is the homologue of the I-shaped support-cells in *Gymnocladus Canadensis*, and of the crystal layer in *Phaseolus vulgaris.* III. Aleurone layer.

Figs. 19, 20 and 21. Isolated palisade cells, macerated in potash; × 175.

Bulletin of the Torrey Botanical Club. Plate LII.



Structure of some Leguminous Seed Coats. L. H. Pammel.

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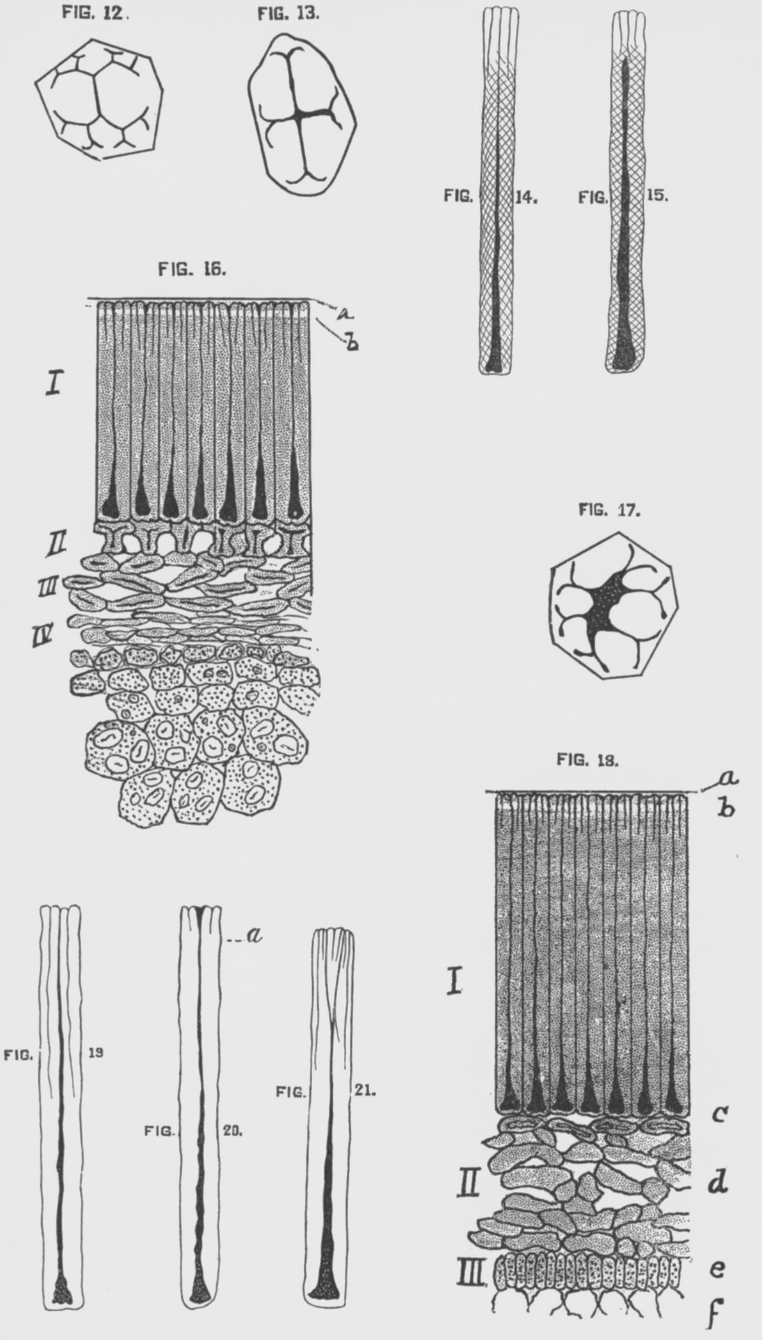

Structure of some Leguminous Seed Coats. L. H. Pammel.